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Seabird use of discards from a nearshore shrimp fishery in the South Atlantic Bight, USA

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Abstract Shrimp trawling is common throughout the southeastern and Gulf of Mexico coasts of the USA and is the primary contributor to fisheries discards in these regions. Tens of thousands of nearshore seabirds nest near shrimp trawling grounds in the USA, but to date, there has been no assessment of the relationship between seabirds and shrimp trawlers. We examined the taxonomic composition of bycatch, rate at which seabirds scavenged bycatch, and energy density of discarded bycatch in a nearshore commercial shrimp fishery. Bycatch was primarily comprised of demersal fish that are not typically accessible to the plunge-diving and surface-feeding seabirds that occur in the area. Hence, seabird diets in the region appear to be broadened taxonomically by the availability of discards. Results from discard experiments indicated that 70% of the nearly 5,500 items discarded by hand were scavenged by seabirds and that the fate of a discarded item was most strongly predicted by its taxonomic order. Laughing gulls scavenged the greatest proportion of discards, although brown pelicans were the only species to scavenge more discards than predicted based upon their abundance. Because this is the first such study in the region, it is difficult to ascertain the extent or intensity of the impact that discards have on nearshore seabirds. Nonetheless, our results suggest that it will be difficult for managers to clearly understand fluctuations in local seabird population dynamics without first understanding the extent to which these species rely upon discards. This may be especially problematic in situations where seabird populations are recovering following natural or anthropogenic stressors.

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Introduction

The ecological relationship between seabirds and commercial fisheries is complex and varies among fisheries, seabird communities, and regions. Research has focused primarily on competition between fisheries and seabirds for forage fish (Furness 2002; Frederiksen et al. 2004) and on the management and mitigation of seabird mortality associated with bycatch (Melvin et al. 2001; Lewison and Crowder 2003). Generally, these interactions have a negative effect on seabird populations either by reducing prey availability or by increasing mortality. In contrast, there are instances where the relationship between seabirds and fisheries may result, at least proximately, in a positive effect on seabird populations. For example, seabirds may

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forage upon discarded bycatch from fisheries (Oro and Ruiz 1997; Arcos and Oro 2001, 2002; Garthe and Scherp 2003), which may increase food availability, the breadth of the diet for scavenging birds (Furness et al. 1992; Camphuysen et al. 1995; Garthe et al. 1996; Navarro et al. 2009), and the distribution and abundance of seabirds (Walter and Becker 1997; Oro and Ruxton 2001).

The commercial shrimp fishery provides an interesting case study of seabird-fisheries interactions. Commercial shrimp trawling is common in nearshore waters around the globe, and these trawlers generate high volumes of discards (Harrington et al. 2005; Kelleher 2005; Gillett 2008). Where shrimp trawling and seabirds overlap spatially and temporally, shrimp trawlers are strong local attractors of nearshore seabirds and discards from shrimp trawlers appear to be common in diet samples collected at colonies (Blaber et al. 1995; Walter and Becker 1997; Wickliffe and Jodice 2010). Because shrimp trawlers discard primarily demersal fish, certain seabird communities (e.g., nearshore gulls and terns, which forage primarily in the uppermost level of the water column) also may realize an enhancement in the breadth of their diet due to the transboundary movement of fish from the benthos to the surface during the trawling and discarding process (Arcos et al. 2002, Jodice and Suryan 2010).

We investigated the use of discards from shrimp trawlers by seabirds in nearshore waters of the South Atlantic Bight (SAB), USA. Commercial shrimp trawling is common, and ports occur regularly along the southeastern and Gulf of Mexico coasts of the USA. Within our study area along the central coast of South Carolina (Fig. 1), the commercial shrimp fleet trawls within 10–30 km of several seabird colonies that support >20,000 breeding brown pelicans (*Pelecanus occidentalis),* laughing gulls (*Larus atricilla*), royal terns (*Thalasseus maxima*), and sandwich terns (*Thalasseus sandvicensis*) each year (Jodice et al. 2007). As a first step in assessing the relationship between seabirds and the shrimp fleet in this region, we examined seabird attendance at trawlers, finding that most attendees were species that were breeding locally and that shrimp trawlers were attended regularly within 20–30 km of colonies (Wickliffe and Jodice 2010). Here, we investigate (1) the taxonomic composition of bycatch from shrimp trawlers, (2) the proportion of bycatch scavenged during discard experiments by each seabird species in relation to seabird abundance at trawlers, (3) the proximate composition and energy density of discarded items, and (4) the relationship between the taxonomic classification of a discarded item and its eventual fate (i.e., scavenged by seabirds or not).

Methods

Study area

Data were collected during commercial shrimp trawls ($n = 39$) during the seabird breeding season (May–August 2006 and 2007) along the central South Carolina coast

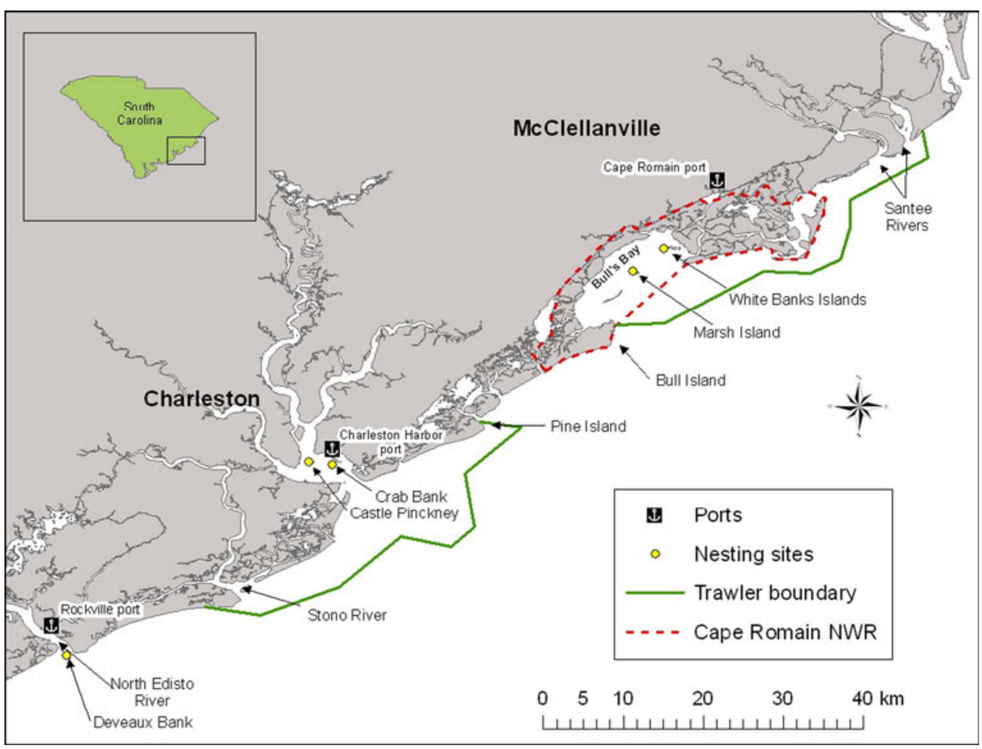

Fig. 1 Locations of commercial shrimp ports and colonies that support nesting brown pelicans, laughing gulls, royal terns, and sandwich terns in and adjacent to Charleston Harbor and Cape Romain National Wildlife Refuge, South Carolina, USA. Studies were conducted from May–August 2006 and 2007. The trawler boundary line represents the area within which all trawls were conducted and all data were collected

adjacent to the mouth of Charleston Harbor and Cape Romain National Wildlife Refuge, South Carolina, USA (hereafter CRNWR or more generally Cape Romain; Fig. 1). Approximately 15 commercial vessels trawled in each region 11–13 km offshore in 3–14 m of water for brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*). Trawlers were 15–21 m in length, towed nets with a 4.7 cm mesh size, and used catch bags with a mesh size of 4.1 cm. Trawl speed was approximately 2.5 knots, and trawl duration was 2–4 h. Each cruise typically included 2–3 hauls day^{-1} and occurred between 0500 h and 1800 h. All tow nets included marine turtle exclusion and bycatch reduction devices.

Our research focused on four species of seabirds: brown pelicans, sandwich terns, royal terns, and laughing gulls. These were the most abundantly breeding seabirds in the region and accounted for >99% of 36,500 birds counted from commercial shrimp trawls during May through August 2006 and 2007 (Wickliffe and Jodice 2010). Details regarding the history, descriptions, and nest counts from each colony appear in Jodice et al. (2007) and Wickliffe and Jodice (2010).

Bycatch composition and discard scavenging rates

We determined the taxonomic composition of trawl bycatch by collecting 4 L of discarded bycatch during each haulback each day (≤4 times day^{-1}). Each collected item ($n = 5{,}428$) was identified to species and measured to ±5 mm before being discarded, set aside for later discard experiments, or frozen for subsequent analysis of energy density and proximate composition in the laboratory.

The fate of discards was determined following procedures described in similar studies (Hudson and Furness 1988; Garthe et al. 1996; Arcos 2001). We selected items 50–600 mm in length as this size range appeared to be the most likely to be consumed by the most common seabirds in the area based on preliminary observations (excluding elasmobranches, echinoderms, cnidarians, and ctenophores). All items collected for discard experiments were used within 30 min of collection or stored on ice to preserve the freshness of the sample until discarded. Individual items were discarded by hand (5 fish min^{-1}) during operational discarding (a focused activity that typically lasted 30 min haul^{-1}) to ensure that an artificial feeding environment was not created by our single discards. The fate of each individually discarded item was classified as scavenged (if so, by the seabird species that did so) or not scavenged (i.e., sinking beneath the surface). Individual birds were not classified by age due to the difficulties of rapidly and accurately assessing age during surveys (e.g., Oro and Ruiz 1997; Garthe and Scherp 2003). Kleptoparasitism was not recorded as this often occurred as birds were flying away from the vessels. Only experiments with >30 items discarded were used for analyses (Garthe and Hüppop 1998).

A foraging success index (SI) was calculated for each species of seabird for each discard experiment (Arcos and Oro 2001). The index ranged from 1 to −1 with a positive value indicating a species of seabird consumed a greater proportion of the bycatch than expected based on that same seabird's abundance. The success index was calculated as

$$\text{success index}_j = \left(O_j - E_j\right)/\left(O_j + E_j\right)$$

where success index$_j$ is the foraging success index for each species j, O_j is the observed number of discarded items consumed by species j, and E_j is the expected number of items taken, estimated by multiplying the total number of items offered by the percent of that species behind the trawler during that discard experiment (Arcos 2001). The abundance of each seabird species was determined via surveys that are detailed in Wickliffe and Jodice (2010) and that were temporally aligned with the start and end time of each discard experiment.

Proximate composition and energy density

Proximate composition and energy density of Atlantic croaker *(Micropogonias undulates)*, spot *(Leiostomus xanthurus),* star drum (*Stellifer lanceolatus*), silver seatrout *(Cynoscion nothus)*, Spanish mackerel (*Scomberomorus maculates*), Atlantic menhaden *(Brevoortia tyrannus),* and broad-striped anchovy (*Anchoa hepsetus*) were measured. These species commonly appear as discarded bycatch during shrimp trawling and are commonly found in diets of seabirds in the region. Fish were dried in a convection oven at 100°C until the mass of each sample remained constant (i.e., ±0.005 g) for >1 day. The percent water content of each fish was calculated as: % water content = [[thawed wet mass (g) − dried mass (g)]/thawed wet mass (g)] * 100. Total lipids were extracted using a soxhlet apparatus and a solvent of hexane/isopropyl alcohol 7:2 (v/v) for ca. 10 h (Radin 1981). Lipid mass was calculated as: lipid mass (g) = dried mass (g)−lean dry mass (g). Lean, dry samples were then ashed in a muffle furnace for 12 h at 600°C, resulting in a sample that was ash-free, lean, and dry. The remaining material consisted almost exclusively of protein. Percent protein was calculated as: % protein content = 100 − (percent moisture + percent lipid + percent ash). The energy density of each sample was calculated as the sum of lipid and protein energy using the energy equivalents of 39.3 kJ g^{-1} for lipid and 17.8 kJ g^{-1} for protein (Schmidt-Nielsen 1997). Energy density was calculated on a wet-mass basis to better assess the value of each fish

Table 1 Composition of bycatch (% of items) collected from Cape Romain (n = 42 hauls) and Charleston Harbor (n = 50 hauls), South Carolina, May–August 2006 and 2007

Taxonomic order	Cape Romain		Charleston Harbor	
Common name (*Genus species*)	2006 n = 1,306	2007 n = 1,195	2006 n = 916	2007 n = 2,011
Perciformes				
Atlantic croaker *(Micropogonias undulatus)*	*22.4**	*33.3*	*7.2*	*18.7*
Spot *(Leiostomus xanthurus)*	*23.6*	*6.1*	*32.0*	*14.7*
Star drum (*Stellifer lanceolatus*)	16.9*	18.3	9.7	12.4
Atlantic cutlassfish *(Trichiurus lepturus)*	7.0	10.6	11.3	10.4
Silver seatrout *(Cynoscion nothus)*	1.4*	3.3	7.8	8.8
Butterfish *(Peprilus triacanthus)*	2.4	1.2	5.4	3.4
Clupeiformes				
Atlantic menhaden *(Brevoortia tyrannus)*	*5.0*	1.9	1.0	0.2
Shannon's diversity index (all items)	2.4	2.3	2.4	2.7

Only species that comprised ≥5% of the bycatch in any location-year are listed (a complete list of species can be found in Wickliffe 2008). Italicized values indicate significant differences ($P < 0.05$) between years within region and an asterisk adjacent to the value listed for Cape Romain 2006 indicates significant differences between regions within years

as obtained by seabirds (Anthony et al. 2000). A detailed description of protocols used to determine proximate composition and energy density can be found in Anthony et al. (2000) and Jodice et al. (2006).

Statistical analysis

A negative binomial regression was used to determine whether there were differences in the frequency of occurrence of Atlantic croaker, Atlantic menhaden, spot, star drum, Atlantic cutlassfish, and silver seatrout between years (2006, 2007) and locations (Charleston Harbor, Cape Romain). One-way ANOVA was used to determine whether there were differences in SIs among the four most common seabird species observed at trawlers (brown pelican, royal tern, sandwich tern, laughing gull). Species diversity of the composition of bycatch in each region and year were calculated with Shannon's Diversity Index.

The extent to which success indices were related to independent variables was assessed using generalized linear models (Table S1), while the relationship between discard fate (scavenged by seabird or not) and a series of independent variables were assessed using logistic regression (Table S2; there was a significant relationship between length and order so these two variables were never placed in the same model). We used the Hosmer–Lemeshow goodness-of-fit test to assess fit for the global logistic regression model. Once each generalized linear or logistic regression model was run, we ranked each based on its AICc statistic (Burnham and Anderson 2002). The AICc weight was interpreted as the probability that the model in question was the best model tested given the data available and models under consideration. Here, we only report models with a >10% chance of being the best model from the candidate set (hereafter "best models"). Model-averaged estimates of coefficients and unconditional estimates of standard errors were calculated following Burnham and Anderson (2002) for variables or interaction terms that were included in best model sets. In some cases, variables included in the best model sets had standard errors that were relatively large compared with the coefficient estimates, and these variables were not discussed. Discard selection was not assessed by species because it was not possible to accurately account for competitive or kleptoparasitic behavior during these experiments.

We conducted a one-way analysis of variance (ANOVA) to test for differences in water, lipid, protein, and energy density among fish species. We used t-tests to examine differences in proximate composition and energy density between fish categorized as demersal (i.e., Atlantic croaker, spot, star drum, and silver sea trout, which occur primarily at or near the bottom of the water column) and as pelagic (i.e., striped anchovy, Atlantic menhaden, and Spanish mackerel which occur primarily in schools closer to the surface). Values for percent water, lipid, and protein were arcsine transformed for all statistical analyses, although raw values are also presented.

Means are reported ± 1 SE, and odds ratios are reported as 95% CIs. For analyses not subjected to model selection, results were considered as significant if $P \leq 0.05$, although actual P values are reported throughout. All statistical analyses were conducted using SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA).

Results

Bycatch composition and discard scavenging rates

We collected 5,428 bycatch items from 37 species of fish and invertebrates from 92 hauls during both years (Table 1). Atlantic croaker, Atlantic cutlassfish, star drum, and spot were the most abundant bycatch items. Species richness ranged from 30 to 34 among location-years, and Shannon's diversity index was similar among the four location-years (Table 1). Atlantic croaker, star drum, and Atlantic menhaden all comprised a greater proportion of the bycatch in Cape Romain ($\chi^2 \geq 6.9$, $P \leq 0.008$ for each), while spot and silver seatrout comprised a greater proportion of the bycatch in Charleston Harbor ($\chi^2 \geq 14.2$, $P \leq 0.001$ for each). Spot and Atlantic menhaden comprised a greater proportion of the bycatch in 2007 ($\chi^2 \geq 4.9$, $P \leq 0.03$ for each), while Atlantic croaker were more common in 2006 ($\chi^2 = 13.22$, $P = 0.001$). Atlantic menhaden, a common prey item for brown pelicans in the southeastern USA (Shields 2002), comprised ≤5% of the bycatch in each area and year. Species in the order Pleuronectiformes (i.e., flatfish) never comprised >5% of the bycatch in any location or year.

Of the 1,705 items discarded during experiments in 2006 and 2007, 77% were perciformes, 11.3% were clupeiformes, 6.2% were pleuronectiformes, and the remainder were from a variety of orders each comprising <2% of the total items discarded during experiments (Table 1). Approximately 69% of the discarded items were taken by seabirds, while 31% sank or were consumed beneath the surface by species other than birds (e.g., blacktip sharks *Carcharhinus limbatus* and bottlenose dolphins *Tursiops truncatus*). Laughing gulls consumed 32.7% of all items scavenged, brown pelicans 21.2%, royal terns 12.6%, and sandwich terns 2.6% (Table 2). Brown pelicans were the only species, which obtained more bycatch than predicted relative to their abundance (SI = 0.29 ± 0.04). The success indices for sandwich terns (−0.60 ± 0.08), royal terns (−0.20 ± 0.05), and laughing gulls (−0.31 ± 0.03) were all negative. The SI of brown pelicans was positively affected by the sum of all birds present, the SI index of sandwich terns was negatively affected by the sum of all birds present, the SI of royal terns tended to decrease with date, and none of the variables we measured had any effect on the success index of laughing gulls (Tables 3 and 4; Table S2).

For each of the seabirds, percifomes comprised 73–84% of the discarded items taken, while clupeiformes comprised 11–20% of the items taken (Table 5). The model that best predicted whether or not an item was consumed by a seabird included the taxonomic order of the item, the study area, and their interaction (model 11, Table S2). There was a 92% probability that this model was the best model given the data collected and models assessed, and the Hosmer–Lemeshow goodness-of-fit test indicated an adequate fit for this model ($P > 0.9$). The probability of any other model we tested being the best model was <4%. To assess the interaction between taxonomic order and study area, we conducted a separate logistic regression for each study area. In Cape Romain, clupeiformes were 5.0–19.7 times as likely to be taken as pleuronectiformes, perciformes were 4.5–14.0 times as likely to be taken as pleuronectiformes, other items were 1.1–4.3 times as likely to be taken as

Table 2 Percent of total discarded items from each taxonomic order taken by each seabird during commercial shrimp trawls operated in nearshore waters of South Carolina, USA, May–August 2006 and 2007

Taxonomic order	Length (mm) range	Number of items discarded	Percent consumed by brown pelicans	Percent consumed by laughing gulls	Percent consumed by royal terns	Percent consumed by sandwich terns
Perciformes	50–595	1,313	23.0	35.3	13.0	2.5
Clupeiformes	55–250	192	20.3	33.8	19.8	4.7
Pleuronectiformes	60–430	105	6.7	10.5	3.8	1.0
Teuthida	50–150	33	9.1	27.3	6.1	6.1
Scorpaeniformes	75–140	30	20.0	16.7	0.0	0.0
Aulopiformes	100–230	17	11.8	17.6	0.0	0.0
Decapoda	11–140	8	0.0	0.0	0.0	0.0
Gadiformes	135–140	3	66.7	33.3	0.0	0.0
Tetraodontiformes	95–130	4	0.0	0.0	0.0	0.0
All items	50–595	1,705	21.2	32.7	12.6	2.6

For example, 1,313 perciformes were offered and of those 23% were taken by pelicans

Table 3 Model selection statistics from models assessing success index of each of the four most common seabirds recorded during shrimp trawling operations in nearshore waters of South Carolina, USA, May–August 2006 and 2007

Species/(model number) model	ΔAICc	AICc weight
Brown pelican		
(2) Seabird abundance		0.31
(19) Julian date within year, seabird abundance	0.8	0.21
Laughing gull		
(1) Intercept only		0.21
(6) Study area	1.2	0.12
(4) Year	1.5	0.10
Royal tern		
(3) Julian date within year		0.17
(1) Intercept only	0.1	0.15
(4) Year	0.9	0.10
Sandwich tern		
(19) Julian date within year, seabird abundance		0.33
(2) Seabird abundance	0.8	0.22

Only models with an AICc weight >0.10 are presented. Model numbers from Table S1

Table 4 Coefficient estimates ± SE for main independent variables related to success index of the four most common seabirds recorded during shrimp trawling in nearshore waters of South Carolina, USA, May–August 2006 and 2007

	Brown pelican	Laughing gull	Royal tern	Sandwich tern
Abundance	*0.002 ± 0.0009*	–	–	*−0.004 ± 0.002*
Date	*0.003 ± 0002*	–	*−0.004 ± 0.002*	*0.005 ± 0.004*
Year (2006)[a]	–	−0.06 ± 0.06	*−0.141 ± 0.105*	–
Study area	–	0.06 ± 0.06	–	–

Only variables occurring in models where AICc weights >0.10 are included in the table. A "–" indicates that the variable was not included in a best model. Variables with SE < coefficient estimates are italicized. Variables with SE > coefficients are also presented because these variables were included in at least one of the best models for a species from Table 3

Coefficient estimates and standard errors calculated via model averaging (see "Methods") when variable included in >1 model from Supplemental Table 1, otherwise derived from single model

[a] The reference level was year = 2007. Therefore, the coefficient estimates are the differences between the variable level in parentheses and the reference level

pleuronectiformes, and clupeiformes were 2.5–8.8 times as likely to be taken as other items. In Charleston Harbor, clupeiformes were 8.7–92.0 times as likely to be taken as pleuronectiformes, perciformes were 7.7–62.6 times as likely to be taken as pleuronectiformes, and clupeiformes were 7.2–166.6 times as likely to be taken as other items.

Proximate composition and energy density

Summary data for energy density as well as the contents of water, lipid, and protein for discarded fish are presented in Table 6. Water content did not differ among species ($F_{(6,38)} = 0.9$, $P = 0.5$), although lipid content ($F_{(6,38)} = 11.1$, $P < 0.0001$) was higher in Atlantic croaker, broad-striped anchovy, and star drum compared with Atlantic menhaden, silver sea trout, Spanish mackerel, and spot. Energy density was generally highest in broad-striped anchovy, Atlantic croaker, and star drum and was least in Atlantic menhaden ($F_{(6,38)} = 6.34$, $P < 0.0001$). There were no significant differences between demersal (drum, spot, croaker, sea trout) and pelagic (menhaden, mackerel, anchovy) species for either water content or energy density ($P > 0.14$ for each), although lipid content was higher, but not significantly so ($t_{38} = 2.0$, $P = 0.06$) in demersal compared with pelagic fish.

Discussion

Bycatch composition and discard scavenging rates

Although there were 30–34 species recorded as bycatch in each year and each location, just four species (i.e., Atlantic croaker, star drum, spot, and Atlantic cutlassfish) comprised on average 16% of the items among years and locations. These species are abundant demersal fish

Table 5 Percent of total items taken by each seabird from each order during commercial shrimp trawls operated in nearshore waters of South Carolina, USA, May–August 2006 and 2007

Seabird	Number taken	Percent Clupeiformes (n = 151/192)	Percent Perciformes (n = 969/1,313)	Percent Pleuronectiformes (n = 23/105)	Percent other items (n = 35/95)
Brown pelican	361	10.8	83.7	1.9	3.6
Laughing gull	557	11.6	83.1	2.0	3.3
Royal tern	215	17.7	79.5	1.9	0.9
Sandwich tern	45	20.0	73.3	2.2	4.4

n = (number taken/number offered during discard experiments)

For example, brown pelicans took 361 discards and of those 84% were perciformes

Table 6 Mean ± (SE) water content, proximate composition (% wet mass), and energy density of forage fish species collected in nearshore waters of coastal South Carolina, USA, May–August 2006 and 2007

Species	Water (%)	Lipid (%)	Protein (%)	Energy density (kJ/g)
Broad-striped anchovy (n = 4)	78.2 ± 1.8	9.0 ± 1.6	15.7 ± 2.0	3.7 ± 0.3
Atlantic croaker (n = 6)	76.1 ± 1.1	11.8 ± 2.5	15.1 ± 0.6	4.1 ± 0.3
Atlantic menhaden (n = 9)	77.6 ± 0.1	2.7 ± 0.7	11.1 ± 1.0	2.9 ± 0.04
Silver seatrout (n = 3)	77.5 ± 0.1	2.0 ± 0.7	13.2 ± 3.2	3.4 ± 0.1
Spanish mackerel (n = 3)	76.8 ± 0.2	2.6 ± 0.3	7.1 ± 2.3	3.6 ± 0.04
Spot (n = 13)	77.7 ± 0.3	2.6 ± 0.4	12.7 ± 1.4	3.2 ± 0.1
Star drum (n = 7)	77.0 ± 0.9	10.3 ± 2.0	11.2 ± 2.5	3.8 ± 0.2

(Miglarese et al.1982; Wenner and Sedberry 1989) and are common bycatch items in shrimp trawls throughout the southeastern USA (FAO 1997). Furthermore, none of the bycatch species are protected or in a restricted fishery, so shrimp trawling would not be limited on their behalf.

Bycatch from demersal trawl fisheries often are comprised of benthic or benthopelegic fish, which may not typically be available to surface- and plunge-diving seabirds (Furness et al. 1992; Camphuysen 1994; Garthe et al. 1996). Although we did not collect diet samples from colonies during this study, demersal fish (e.g., spot, drum) have been recorded in diets of brown pelicans (Shields 2002) and royal and sandwich terns (McGinnis and Emslie 2001) within the region. Therefore, it appears that discards from shrimp trawling result in a broadening of the diet for surface-feeding and plunge-diving seabirds in the region.

During our study, seabirds consumed ca. 70% of discarded items offered, similar to rates documented in other trawler studies (Oro and Ruiz 1997; Walter and Becker 1997; Martinez-Abrian et al. 2002). Although discards can float for many hours (Blaber et al. 1995), that does not appear to be the case at the South Carolina shrimp trawl fishery. Here, sharks (primarily blacktip sharks, *Carcharhinus limbatus*) and bottlenose dolphins (*Tursiops truncatus*) were common at trawlers (although not quantified) and appeared to consume many of the discarded items that sank. Therefore, discards from this fishery appear to be a short-lived food resource for scavenging seabirds.

Laughing gulls were the most common seabird we observed at trawlers, comprising 65% of the birds counted (Wickliffe and Jodice 2010), and they consumed the highest proportion of discarded items offered both among and within taxa. Gulls are often the numerically dominant seabird at trawlers particularly in nearshore systems (Walter and Becker 1997; Garthe and Scherp 2003). Gulls did, however, take fewer discards than predicted based on their abundance throughout the study period and this appears to be common in other regions as well (Garthe and Hüppop 1994; Arcos 2001). Gulls frequently attempted to kleptoparasitize discarded items from other seabirds. Because we were not able to quantify the success of kleptoparasitism, it is likely that the SI of gulls was actually higher than what we estimated. Nevertheless, the abundance of gulls at trawlers and the proportion of items they consumed demonstrate substantial use of discarded items by this species.

Royal and sandwich terns were observed frequently at trawlers but comprised only 19 and 6% of the total birds counted, respectively (Wickliffe and Jodice 2010). During our study, both terns captured fewer discards than predicted based on their abundance and this appears to be common for terns as a group (Garthe and Hüppop 1994; Arcos 2001). Both tern species appeared to take Clupeiformes, a common item in their natural diets, more frequently compared with other discarded items. Success indices for terns may be relatively low because they tend to be specialized foragers and single-prey loaders (Furness et al. 1988; Arcos et al. 2002). Competition with larger or more aggressive species also may negatively affect their success rates, particularly for the smaller sandwich tern when the density of birds at trawlers is high. Although terns do not appear to be efficient scavengers of discards, their frequency of attendance at trawlers does appear to be high (Yorio and Caille 1999; Martinez-Abrian et al. 2002; Valeiras 2003; Wickliffe and Jodice 2010), suggesting some benefit is accrued by individuals.

No other studies have reported on the attendance of pelicans at discarding vessels. Pelicans comprised 10% of the birds we counted at trawlers (Wickliffe and Jodice 2010), captured 21% of the items offered, and were the only species with a positive SI. Pelicans may be relatively efficient at capturing discarded items in this fishery because they utilize multiple foraging strategies (surface-seizing and plunge-diving), can access prey both at and beneath the surface, can consume prey across a large size range, and are not single-prey loaders (i.e., can forage at a location for extended periods of time; Shields 2002). The positive relationship between the SI of pelicans and the sum of birds present appears to result from their ability to successfully seize prey from the surface when the density of seabirds at trawlers, and hence competition, increases.

Discard fate was most strongly affected by taxonomic order. Clupeiformes and perciformes were commonly selected in both study areas. Clupeiformes constitute a substantial portion of the natural diets of brown pelicans, royal terns, and sandwich terns (McGinnis and Emslie 2001; Shields 2002). Pleuronectiformes (i.e., flatfishes, not a typical diet item) were unlikely to be scavenged from discards by seabirds. The apparent preference for clupeiformes and perciformes compared with pleuronectiformes may be due to differences in the shape of the body between these two orders. Walter and Becker (1997) found that round-bodied prey such as clupeiformes and perciformes were consumed more frequently.

Despite being readily scavenged from discards, clupeiformes comprised <6% of the bycatch we sampled. It appears, therefore, that seabirds would be unlikely to scavenge at trawlers specifically for clupeiformes, a common, natural diet item for each of these seabirds. However, small and medium-sized perciformes, which were consumed readily by seabirds during discard experiments, represented a much larger portion of the bycatch sample (66.5%). Although demersal perciformes may not be a common item in the natural diet for these four seabird species in the region, the relative abundance of this group as discarded bycatch and their round body shape may make them an acceptable alternative diet item. For example, perciformes comprised over 40 and 10% of diet items fed to chicks of royal and sandwich terns, respectively, in one North Carolina study (McGinnis and Emslie 2001).

Proximate composition and energy density

Although our sample size of fish was low for these analyses and hence results should be interpreted cautiously, few other data are available on energy density or proximate composition of forage fish from this region (Gooch et al. 1987). The range in energy density among discarded taxa was relatively narrow in this study, and the energy density and protein content of demersal species were slightly higher compared with pelagic species. In contrast, energy density of forage fish from higher latitudes can range greater than fivefold and is often greater in pelagic compared with demersal species (Anthony et al. 2000). Narrow ranges in energy density may be more common in low-lipid fish from warm-water regions where annually food is relatively stable compared with higher latitudes (Stickney and Torres 1989). Our data suggest that seabirds scavenging on discards did not face a wide range in diet quality nor was the discard process supplying seabirds with low-quality forage fish, or junk-food (Jodice et al. 2006; Grémillet et al. 2008). Other studies have found, however, that demersal fish made available through trawler discards can contain higher contaminant levels compared with pelagic species, and in this way, the discarding process functionally moves contaminants across ecological boundaries and makes these contaminants accessible to predators that would not normally be exposed (Monteiro et al. 1996; Arcos et al. 2002; Jodice and Suryan 2010). Although proximate composition and energy density can change as samples become dehydrated or spoil, bycatch in our study was usually discarded soon after haulback and consumed rapidly leaving little opportunity for deterioration of quality.

Conclusions

Pelicans, terns, and gulls successfully foraged upon discarded bycatch provided by shrimp trawlers during the seabird breeding season and captured approximately 70% of the bycatch discarded in experiments. Most of the items taken by these surface-feeding and plunge-diving seabirds were demersal fish and hence not likely to be common natural diet items. Our limited data suggest that discards do not create a junk-food scenario with respect to diet quality, although larger sample sizes and seasonally varied samples would benefit such an assessment.

Because this study was one of the first to examine the relationship between seabirds and discarded bycatch in this region, our understanding of this interaction remains quite basic. Although we documented that seabirds regularly attend trawlers (Wickliffe and Jodice 2010) and that a large proportion of discarded bycatch is scavenged by seabirds, the contribution of these items to adult diets and chick diets remains unknown. There is also a lack of data on the total mass of discards available and the number of vessels operating within the fleet, although the fishery has experienced a decline over the past decade due primarily to economic factors (SAFMC 2009). Nonetheless, shrimp fisheries are common in the southeastern and Gulf of Mexico regions of the USA, are the primary contributor to discards in these regions, and have relatively large ratios of discard biomass to landing biomass (Harrington et al. 2005; SAFMC 2009). Therefore, the impact of the fleet on seabirds may be great and needs to be considered in the management of nearshore marine systems. This may be particularly relevant when assessing seabird population dynamics, which we were unable to address due to a lack of long-term datasets (e.g., diet, productivity, discard rates). Ultimately, an energetics-based analysis that considers not only the cost of seabird foraging but also the energetic value and availability of prey may best elucidate the ecological relationship between seabirds and discards in the region and hence provide the greatest opportunity to understand the management and conservation implications of the dynamics of the shrimp fleet on locally breeding seabirds. Such an assessment may be particularly relevant following natural and anthropogenic stressors or catastrophes.

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References

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J Exper Mar Biol Ecol 53:53–78

Arcos JM (2001) Foraging ecology of seabirds at sea: significance of commercial fisheries in the NW Mediterranean. PhD thesis, University of Barcelona, Spain. http://tdcat.cesca.es/TDCat-0219102-114337/index.html

Arcos JM, Oro D (2001) Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater *Puffinus mauretanicus*. Mar Ecol Prog Ser 239:209–220

Arcos JM, Oro D (2002) Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). Mar Biol 141:277–286

Arcos JM, Ruiz X, Bearhop S, Furness RW (2002) Mercury levels in seabirds and their fish prey at the Ebro Delta (NW Mediterranean): the role of trawler discards as a source of contamination. Mar Ecol Prog Ser 232:281–290

Blaber SJM, Milton DA, Smith GC, Farmer MJ (1995) Trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. Mar Ecol Prog Ser 127:1–13

Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer, New York

Camphuysen CJ (1994) Flatfish selection by herring gulls *Larus argentatus* and the lesser black-backed gulls *Larus fuscus* scavenging at commercial beam trawlers in the southern North Sea. Neth J Sea Res 32:91–98

Camphuysen CJ, Calvo B, Durinck J, Ensor K, Follestad A, Furness RW, Garthe S, Leaper G, Skoy H, Tasker ML, Winter CJN (1995) Consumption of discards by seabirds in the North Sea. Neth J Sea Res 5:202

FAO (1997) FAO technical guidelines for responsible fisheries—fisheries management, vol 4. Rome

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson NJ (2004) The role of industrial fisheries and environmental change in the decline of North Sea black-legged kittiwakes. J Appl Ecol 41:1129–1139

Furness RW (2002) Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. ICES J Mar Sci 59:261–269

Furness RW, Hudson AV, Ensor K (1988) Interactions between scavenging seabirds and commercial fisheries around the British Isles. In: Burger J (ed) Seabirds and other marine vertebrates: competition, predation, and other interactions. Columbia University Press, New York, pp 240–268

Furness RW, Ensor K, Hudson AV (1992) The use of fishery waste by gull populations around the British Isles. Ardea 80:105–113

Garthe S, Hüppop O (1994) Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Mar Ecol Prog Ser 106:1–9

Garthe S, Hüppop O (1998) Possible biases in experiments evaluating the consumption of discards by seabirds in the North Sea. Mar Biol 131:735–741

Garthe S, Scherp B (2003) Utilization of discards and offal from commercial fisheries by seabirds in the Baltic Sea. ICES J Mar Sci 60:980–989

Garthe S, Camphuysen CJ, Furness R (1996) Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar Ecol Prog Ser 136:1–11

Gillett R (2008) Global study of shrimp fisheries. FAO Document technique sur les pêches. No. 475. FAO, Rome

Gooch JA, Hale MB, Brown T Jr., Bonnet JC, Brand CG, Regier LW (1987) Proximate and fatty acid composition of 40 southeastern U.S. finfish species. NOAA/National Marine Fisheries Service, NOAA Technical Report NMFS 54

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJ, Ryan PG (2008) A junk-food hypothesis for gannets feeding on fishery waste. Proc Royal Soc Lond 275:1149–1156

Harrington J, Myers R, Rosenberg A (2005) Wasted fishery resources: discarded bycatch in the USA. Fish Fish 6:350–361

Hudson AV, Furness RW (1988) Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland. J Zool 215:151–166

Jodice PGR, Suryan RM (2010) The transboundary nature of seabird ecology. In: Trombulak S, Baldwin R (eds) Landscape scale conservation planning. Springer, New York, pp 139–166

Jodice PGR, Roby DD, Turco KR, Suryan RM, Irons DB, Piatt JF, Shultz MT, Roseneau DG, Kettle AB, Anthony JA (2006) Assessing the nutritional stress hypothesis: the relative influence of diet quantity and quality on seabird productivity. Mar Ecol Prog Ser 325:267–279

Jodice PGR, Murphy TM, Sanders FJ, Ferguson LM (2007) Longterm trends in nest counts of colonial nesting seabirds in South Carolina USA. Waterbirds 30:40–51

Kelleher K (2005) Discards in the world's marine fisheries—an update. FAO fisheries technical paper 470. FAO, Rome

Lewison RL, Crowder LB (2003) Estimating fishery bycatch and effects on a vulnerable seabird population. Ecol Appl 13:743–753

Martinez-Abrian A, Mastre R, Oro D (2002) Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. ICES J Mar Sci 59:529–537

McGinnis TW, Emslie SD (2001) The foraging ecology of royal and sandwich terns in North Carolina, USA. Waterbirds 24:361–370

Melvin EF, Parrish JK, Dietrich KS, and Hamel OS (2001) Solutions to seabird bycatch in Alaska's demersal longline fisheries. Washington Sea Grant Program. ASG-AS 01-01

Miglarese JV, McMillan CW, Shealy MH Jr (1982) Seasonal abundance of Atlantic croaker (*Micropogonias undulatus*) in relation to bottom salinity and temperature in South Carolina estuaries. Estuaries 5:216–223

Monteiro LR, Costa V, Furness RW, Santos RS (1996) Mercury concentrations in prey fish indicate enhanced bioaccumulation in mesopelagic environments. Mar Ecol Prog Ser 141:21–25

Navarro J, Louzao M, Arcos JM, Delgado A, Hobson KA, Oro D, Genovart M, Igual M, Forero MG (2009) Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. Mar Biol 156:2571–2578

Oro D, Ruiz X (1997) Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. ICES J Mar Sci 54:695–707

Oro D, Ruxton G (2001) The formation and growth of seabird colonies: Audouin's gull as a case study. J Anim Ecol 70:527–535

Radin NS (1981) Extraction of tissue lipids with a solvent of low toxicity. Meth Enzymol 72:5–7

Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment, 5th edn. Cambridge University Press, Cambridge

Shields M (2002) Brown Pelican (*Pelecanus occidentalis*). In: Poole A, Gill F (eds) The birds of North America, No.609. The Birds of North America, Inc., Philadelphia

South Atlantic Fishery Management Council (2009) Fishery ecosystem plan volume III—human and institutional environment. Charleston, South Carolina. http://www.safmc.net/ecosystem/Home/EcosystemHome/tabid/435/Default.aspx

Stickney DG, Torres JJ (1989) Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico. Mar Biol 103:13–24

Valeiras J (2003) Attendance of scavenging seabirds at trawler discards off Galicia, Spain. Scientia Marina 67(S):77–82

Walter U, Becker PH (1997) Occurrence and consumption of seabirds scavenging on shrimp trawler discards in the Wadden Sea. ICES J Mar Sci 54:684–694

Wenner CA, Sedberry GR (1989) Species composition, distribution, and relative abundance of fishes in the coastal habitat off the Southeastern United States. NOAA Technical Report. NMFS 79

Wickliffe LC (2008) Foraging ecology of seabirds in relation to commercial shrimp trawler activity. Master thesis, Clemson University, Clemson

Wickliffe LC, Jodice PGR (2010) Abundance of nearshore seabirds at shrimp trawlers in South Carolina. Mar Ornith 37:31–39

Yorio P, Caille G (1999) Seabird interactions with coastal fisheries in northern Patagonia: use of discards and incidental captures in nets. Waterbirds 22:207–216